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Assessment of the Maine Lobster Fishery with Surplus Production Models

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Abstract.—A long series of catch and effort data was available for assessment of the impact of fishing on the American lobster (*Homarus americanus*) population off the coast of Maine and the data indicated both the ascending and descending limbs of the equilibrium stock production curve. The logistic and the Fox surplus production models were applied and both models accounted for most of the observed variation in yield in terms of variation in fishing effort and stock biomass. Although the catch data appear to indicate a developing fishery, both models indicated that stock biomass was severely depleted in 1928 when continual collection of annual catch and effort data began. There was little difference between the equilibrium stock production curves of the two models below the optimum level of exploitation but, for high levels of effort, the logistic model predicted a rapid decrease in equilibrium yield with increasing effort whereas the Fox model predicted a slow decline in equilibrium yield with increasing effort. The data were not adequate to clearly identify which model more accurately describes the fishery. Although the models account for most of the variation in yield, additional factors such as a changing environment and changes in regulations also may be important.

In order to assess the Maine fishery for American lobster (*Homarus americanus*), Dow et al. (1975) applied a parabola to describe the equilibrium catch and effort relation. This approach was simple but it did not provide estimates of population parameters and did not enable estimation of yield or stock biomass as functions of time. The catch and effort data for the Maine lobster fishery are suitable for application of surplus production models and, unlike data for other fisheries to which the surplus production model has been applied (e.g., Schaefer 1954, 1957; Fox 1970; Gulland 1972; Ricker 1975; Jensen 1976, 1978; MacCall et al. 1976; Marchesseault et al. 1976), the data for the Maine lobster fishery appear to indicate both the ascending left limb of the equilibrium stock production curve and the descending right limb.

The logistic surplus production model and the model based on the Gompertz equation (Fox 1970) were fitted to the lobster data of 1928 to 1972 and the results were compared with those obtained by Dow et al. (1975). The results obtained with the models also were compared with more recent catch and effort data. Application of the surplus production models revealed interesting aspects of the fishery that were not discovered from empirical analysis of the catch and effort data with a parabola.

Review of the Models

For surplus production models, the capacity of a population to increase is a function of population size, and the maximum capacity to increase occurs at some intermediate population size. A commonly applied surplus production model is the logistic model developed by Volterra (1928), Graham (1935), and Schaefer (1954, 1957) which is described by the equations

$$dY/dt = qEB \quad \text{and} \tag{1}$$

$$dB/dt = kB - kB^2/B_\infty - qEB; \tag{2}$$

Y = yield from the fishery in tonnes;
t = time;
q = catchability coefficient;
B = stock biomass in tonnes;
k = population growth coefficient;
B_∞ = environmental carrying capacity in tonnes;
E = fishing effort.

Under equilibrium conditions the relation between annual yield and effort predicted by equation (2) is the parabola

$$Y_e = qEB_\infty - (q^2B_\infty/K)E^2, \tag{3}$$

where Y_e is the annual equilibrium yield. A maximum sustainable yield (MSY) of $kB_\infty/4$ occurs at a fishing effort of $k/2q$.

If the stock production curve of a fishery is asymmetrical and the yield is slowly decreasing with exploitation beyond the MSY, the surplus production model based on the Gompertz growth equation may give a more accurate description of

TABLE 1.—Parameter estimates for the logistic and Fox surplus production models for the Maine American lobster catch of 1928–1972.

Parameter	Logistic	Fox
k	0.50	0.35
B_∞	8×10^4	8×10^4
q	0.3×10^{-6}	0.4×10^{-6}
R^2	0.83	0.82
SS_{RES}[a]	0.74×10^8	0.88×10^8

[a] Residual sum of squares.

the fishery (Fox 1970). The surplus production model is then given by the equations (Fox 1970)

$$dY/dt = qEB \quad \text{and} \tag{4}$$

$$dB/dt = kB(\log_e B_\infty - \log_e B) - qEB, \tag{5}$$

where all of the terms are defined as for the logistic model. This model will be termed the Fox model. At equilibrium, the relation between annual yield and effort is

$$Y_e = qE \exp(\log_e B_\infty - qE/k), \tag{6}$$

and a MSY of kB_∞/e occurs at a fishing effort of k/q.

Estimation of the parameters of surplus production models with only catch and effort data is difficult. Some methods that have been proposed are an equilibrium approximation (Gulland 1972), linearization (Schaefer 1957; Pella and Tomlinson 1969; Schnute 1977), and nonlinear least squares (Pella and Tomlinson 1969). Although linearization sometimes works, it often gives negative estimates for B_∞, k, or q and equilibrium methods do not give estimates of the catchability coefficient; in general, the best approach is nonlinear least squares (Pella and Tomlinson 1969). Nonlinear least squares requires more computing but, with the wide availability of computers, nonlinear least squares is becoming the standard method for estimation of parameters for nonlinear models and it was the method applied in this study. Values of the parameters that minimized the residual sums of squares between observed and predicted yields were found by a computer search routine similar to that of Pella and Tomlinson (1969).

Data Sources

Catch and effort data for the Maine lobster fishery were given by Dow et al. (1975, Appendix B). The measure of effort is the total number of traps fished but catch per unit of effort of set-over traps is higher than that for daily traps. The catch rate of legal-size American lobsters increases asymptotically with soak time (Fogarty and Borden 1980). Some catch data were available for years prior to 1928 but continual records for annual catch and effort were collected beginning in 1928. Dow et al. (1975) presented data for 1928–1972. Data now are available for 1973–1976 (Anonymous 1973, 1974, 1978, 1980) but, to obtain results comparable to those of Dow et al. (1975), the surplus production models were fitted only to the observations for 1928–1972. The more recent data were used to evaluate and compare the models.

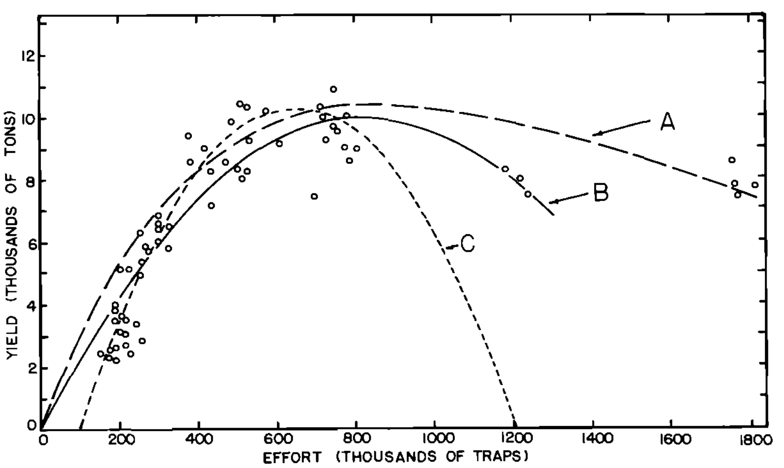

FIGURE 1.—Observed catch (metric tons) and effort data for the Maine American lobster fishery, 1928–1976. Years generally increase from left to right; the three points near the right end of curve B are 1970–1972 and the four points at the right end of curve A are 1973–1976. The curves fitted to the 1928–1972 data are: (A) stock–effort relation for Fox surplus production model, (B) stock–effort relation for logistic model, and (C) parabola fitted by Dow et al. (1975).

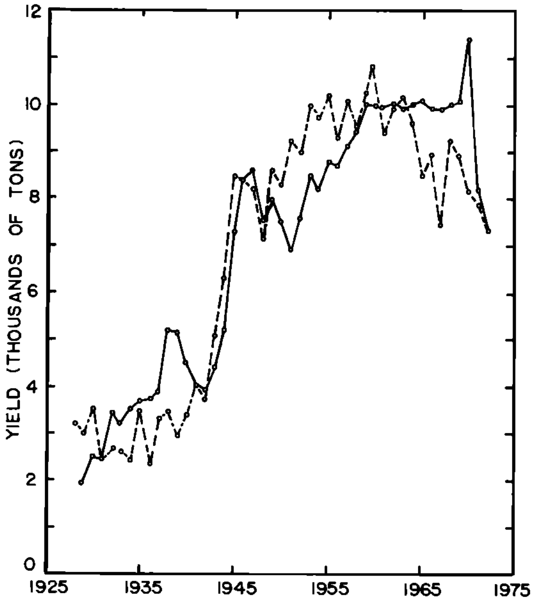

FIGURE 2.—Observed yield of American lobsters (metric tons, dashed line) and yield predicted with logistic surplus production model (solid line).

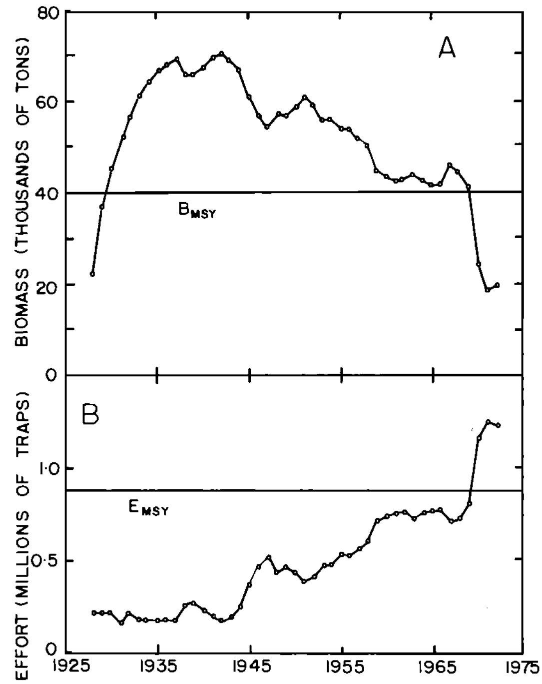

FIGURE 3.—Biomass of the American lobster population predicted with the logistic surplus production model (A), and observed effort (B). The B_{MSY} and the E_{MSY} are the maximum sustained yield of biomass (tonnes) and fishing effort, respectively.

Results

The parameter estimates are listed in Table 1. The logistic model fits the data slightly better than the Fox model, but both account for most of the variation in yield with coefficients of determination (R^2) of 0.83 and 0.82. The catchability coefficients (q) are somewhat different for the two models but the carrying capacities (B_∞) are the same.

To assess the fishery, Dow et al. (1975) fitted a parabola to the catch and effort data; the resulting equation was

$$Y_a = -3{,}824.64 + 42.93E - 0.03285E^2, \quad (11)$$

where Y_a is annual yield in tonnes and E is effort in thousands of traps. The coefficient of determination is higher for the parabola ($R^2 = 0.91$) than for the surplus production models. The parabola has an additional parameter and 56 observations could be applied for fitting it, whereas only 45 observations could be applied for the surplus production models because they need continuity through time.

Observations are located on both the ascending left limbs of the stock production curves and on the descending right limbs of the curves where exploitation is high (Figure 1). With the logistic surplus production model, the maximum sustainable yield is about 10,000 tonnes at a fishing effort of 833,333 traps. The maximum sustainable yield is 10,301 tonnes at a fishing effort of 875,000 traps with the Fox model. For the parabola fitted by Dow et al. (1975), the MSY is 10,200 tonnes, which is higher than the MSY for the logistic surplus production model. With the parabola, the fishing effort at the MSY is 653,425 traps—somewhat less than for the surplus production models.

Discussion

The equilibrium stock production curves of the surplus production models are considerably different from each other and from the parabola (Figure 1). The parabola fits the observations well on the ascending left limb of the data, but it does not pass through the origin, misses completely the observations at higher fishing effort, and is somewhat too high at the dome, giving the contradictory result that yield is below the MSY when fishing effort is above the level that should produce the MSY. The stock production curve of the logistic model does not fit the early data along the ascending left limb but passes through the 1970 to 1972 observations during which fishing effort was high. The stock production curve of the Fox model also does not fit well along the ascending left limb of the curve, and it is too high at the dome, but it is the only curve that gives reasonable predictions of yield for recent years when effort increased greatly. However, the curve describes equilibrium yield, and a large increase in effort should have produced yields higher than those of the equilibrium curve.

The main advantages of the parabola applied by Dow et al. (1975) are that the MSY and optimum effort can be estimated without explicitly describing the dynamics of the population, and the model parameters can be estimated with multiple linear regression. The disadvantages of the parabola are that it does not explain why there should be a maximum yield and the parameters have no biological meaning. The assumptions necessary to apply surplus production models are difficult to verify but these models require only a gross understanding of the dynamics of a population. With surplus production models, yield and stock biomass can be estimated, and these give a more detailed description of a population's response to exploitation.

The parabola indicated slight overfishing in terms of effort (Figure 1) whereas the surplus production models indicated that the fishery had just attained the vicinity of the MSY. The models indicated that, in terms of yield, the fishery was not overexploited and that it had only begun to approach the MSY in the late 1960s. However, factors such as time lags (Marchessault et al. 1976) and stochastic variation (Beddington and May 1977) decrease the MSY and a more detailed assessment of the fishery might indicate that it became overexploited earlier.

The estimates of yield and biomass were similar for the logistic and Fox models; however, just the predictions of the logistic model will be examined to describe the dynamics of the fishery. The logistic model predicts the overall trend of yield (Figure 2) but the residuals are not random; the model overestimates yield during the early years, underestimates yield during the late 1940s and early 1950s and then again overestimates yield in the late 1960s. These trends in the residuals indicate that the American lobster population is acted upon by factors other than the fishery.

The catch and effort data alone gave little clue as to the state of the lobster population in 1928 but the biomass estimates obtained with the biomass equation (Jensen 1984) indicated that, during this early period, the lobster fishery was recovering from either overfishing or a natural calamity (Figure 3). Early catch records are incomplete, but they show that the lobster fishery was heavily exploited prior to 1928. The catch in 1880 was 5,457 tonnes and in 1887 the all time record catch of 11,091 tonnes was established; catch then declined over a period of 15 years (Dow et al. 1975). An extensive trade of egg-bearing females and sublegal-sized lobster also occurred prior to the 1930s. The equilibrium stock production curves may not have fitted the early data (Figure 1) because the fishery was not a developing fishery but rather was recovering from serious overexploitation.

Biomass was low in 1928 and increased gradually into the late 1930s during a period when catch and effort remained low. In the early 1940s, fishing effort began to increase gradually and biomass began to decrease gradually. This pattern continued until 1971. A sharp increase in fishing effort occurred in 1971 and the surplus production models both indicated that a sharp decrease in biomass also occurred; these changes in biomass and effort were not accompanied by an increase in catch. If biomass decreased as predicted, it was not a direct result of biomass removal by the fishery. The decrease in biomass and yield could have resulted from a recruitment failure. The lobster fishery is dependent on recruitment, with 80% or more of the annual catch consisting of new recruits (Dow et al. 1975). In this situation, a large decrease in recruitment would have an immediate, large impact on stock biomass and yield.

The surplus production models give a reasonable description of the American lobster fishery, but the data for the fishery prior to 1928 (together with later data) indicate that there were large, gradual fluctuations in yield that occurred over many years. This variation is not explained by the surplus production models, which limits application of the models for routine management of the fishery. These long-term trends also would not be accounted for by other surplus production models (Pella and Tomlinson 1969; Marchessault et al. 1976; Beddington and May 1977; Deriso 1980) or the analytical model of Beverton and Holt (1957).

Long-term variation in yield could result from variation of environmental parameters. There is an association between the Maine lobster catch and water temperatures at Boothbay Harbor, Maine (Dow 1969, 1977; Dow et al. 1975). From 1929 to the early 1950s, mean annual water temperature increased from about 6°C to 11°C at Boothbay Harbor. This was the period during which the model predicted an increasing biomass, and during this period catch and effort were both increasing. Temperature began to decrease a few years later and biomass also began to decrease. Effort, however, continued to increase substantially and yield decreased slowly. Stock biomass could have increased during the early period because environmental conditions were favorable for survival, then have decreased when conditions for survival became less favorable.

The high correlation between sea surface temperature and recruitment of lobster reported by Dow (1969) and Dow et al. (1975) occurs only in the Gulf of Maine (Harding et al. 1983) and does not appear to be a general phenomenon. Harding et al. (1983) showed that a hypothesis proposed earlier by Huntsman (1923) gave a better account of lobster dynamics over a wide area. Huntsman (1923) proposed that warm surface waters in the summer are necessary for rapid growth and molt completion of planktonic larvae before winter cooling occurs. The hypotheses of Huntsman (1923) and Dow (1969) both accounted for long-term change in lobster abundance in terms of changes in climate. However, the intensity of fishing was very high and the possibility that heavy fishing either caused or facilitated the long-term variation in yield should not be completely discounted. Other factors may have affected the reported catches of lobster. Changes in regulations, methodologies, and enforcement may be important; for example, changes in regulations have resulted in subsequent changes in catch (Thomas 1973).

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